Signaling *via* Water Currents in Behavioral Interactions of Snapping Shrimp (*Alpheus heterochaelis*)

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Abstract. The snappping shrimp *Alpheus heterochaelis* produces a variety of different water currents during intraspecific encounters and interspecific interactions with small sympatric crabs (*Eurypanopeus depressus*). We studied the mechanisms of current production in tethered shrimp and the use of the different currents in freely behaving animals. The beating of the pleopods results in strong posteriorly directed currents. Although they reach rather far, these currents show no distinctions when directed toward different opponents. Gill currents are produced by movements of the scaphognathites (the exopodites of the second maxillae) and can then be deflected laterally by movements of the exopodites of the first and second maxillipeds. These frequent but slow lateral gill currents are most probably used to enhance chemical odor perception. The fast and focused, anteriorly directed gill currents, however, represent a powerful tool in intraspecific signaling, because they reach the chemo- and mechanosensory antennules of the opponent more often than any other currents and also because they are produced soon after previous contacts between the animals. They may carry chemical information about the social status of their producers since dominant shrimp release more anterior gill currents and more water jets than subordinate animals in intrasexual interactions.

Introduction

Alpheus heterochaelis of the family Alpheidae (Decapoda, Caridea) is one of the largest snapping shrimp, reaching a body length of up to 55 mm. It shows a large, modified

snapper claw on one (left or right) side and a small pincer claw on the other side in both sexes (Williams, 1984). The snapper claw allows the animals to produce an extremely fast water jet (of up to 25 m/s; Versluis *et al.*, 2000) by rapid claw closure after cocking the claw in the open position (Ritzmann, 1974). The high velocity of the water jet results in a pressure drop below vapor pressure that causes a cavitation bubble to grow to a size of about 3.5 mm in front of the snapper claw. The collapse of this bubble (and not as previously supposed the mechanical contact of both claw surfaces) causes the extremely loud (up to 215 dB re 1 μPa at 1 m distance; Schmitz, 2001) and short (about 500 ns) snapping sound (Versluis *et al.*, 2000). The strong effect of the water jet and the cavitation bubble collapse can be seen during interspecific encounters. Small prey (*e.g.*, worms, goby fish, or shrimp) can be stunned or even killed by the jet (MacGinitie, 1937; MacGinitie and MacGinitie, 1949; Morris *et al.*, 1980; Suzuki, 1986; Downer, 1989), and interspecific opponents (*e.g.*, small sympatric crabs, *Eurypanopeus depressus*) can be injured at interaction distances of on average 3 mm (Schultz *et al.*, 1998). Toward conspecifics the water jet was not observed to cause any damage but functions as a communicative signal (Herberholz and Schmitz, 1999), both opponents ensuring an interaction distance of on average 9 mm (Schmitz and Herberholz, 1998), which is far enough away from danger caused by implosion of the cavitation bubble. This hydrodynamic signal is analyzed by the receiving shrimp predominantly with the help of mechanosensory hairs on the snapper claw, and may contain information about the strength, motivation, and sex of the snapper (Herberholz and Schmitz, 1998; Herberholz, 1999).

The still rather small interaction distance of less than 1 cm in agonistic encounters between two snapping shrimp

also favors the exchange of chemical signals between the opponents. The literature on chemical orientation and communication in snapping shrimp is limited: Hazlett and Winn (1962) tested aggressive and defensive responses of *Synalpheus hemphilli* to crushed male or female extract, and Schein (1975) and Hughes (1996) investigated the choice of *Alpheus heterochaelis* toward extracts of male or female water in Y-maze experiments without clear-cut results. On the other hand, ablation of the chemosensitive antennules in *Alpheus edwardsii* strongly reduced pair formation and sex recognition, which may be due to impeded distant or contact chemoreception since the pairing frequency remained high when only the antennae were ablated (Jeng, 1994).

The importance of olfactory signals during hierarchy formation was shown in male American lobsters (Karavanich and Atema, 1998a). In these experiments, the recognition of urine-carried chemical signals, which were received by the antennules, allowed the subordinate animal to avoid the familiar dominant shrimp, and therefore reduced the duration and aggression of fights. The exchange of chemical signals is also assumed to play a major role in individual recognition and memory in male and female *Homarus americanus* (Karavanich and Atema, 1998b; Berkey and Atema, 1999). In lobsters, urine is released through a paired set of nephropores on the ventral sides of the basal segments of the second antennae (Parry, 1960). Agonistic behavior in lobsters causes an increase in the probability and volume of urine release (Breithaupt *et al.*, 1999). The released urine is then carried by the powerful anteriorly directed gill currents and may therefore transfer chemical information from one animal to another (Atema, 1985). In recent studies (Zulandt Schneider *et al.*, 1999; Zulandt Schneider and Moore, 2000), chemical cues were also described as an important source for recognition of the dominance status or stress condition of conspecifics in another crustacean, the red swamp crayfish (*Procambarus clarkii*).

In light of these examples, a similar mechanism of chemical signal exchange *via* gill currents in snapping shrimp seems likely. We cannot, however, exclude the possibility that the animals also exchange hydrodynamic signals. In fact, it has been shown that the antennules of crayfish (Mellon, 1996) and lobsters (Guenther and Atema, 1998; Weaver and Atema, 1998) are equipped with both chemical and mechanosensory receptors, and detailed morphological studies of antennule sensory hairs favor the same situation in snapping shrimp (Schmitz, unpubl. obs.). Therefore, snapping shrimp may also perceive hydrodynamic stimuli as well as chemical stimuli with their antennules. Previous studies (Herberholz and Schmitz, 1998, 1999) have shown that the transfer of hydrodynamic signals is realized by the powerful water jet that is formed by rapid closure of the large claw. In contrast, the much weaker gill currents appear to be more suitable for transferring chemical information.

Suspended plastic particles were successfully used to visualize and quantify biological flow fields in lobsters and crayfish in a series of experiments by Breithaupt and Ayers (1996, 1998). Small floating particles of the same density as seawater were added to the aquarium water and illuminated in a horizontal or vertical plane in the vicinity of a tethered animal. Flow fields were then analyzed by tracking individual particles. It was shown that both lobsters and crayfish produce a great variety of flow fields by using the exopodites of the maxillipeds and by fanning the pleopods. The latter was also discussed with respect to chemical communication: male American lobsters commonly fan their pleopods at the second entrance of their shelter, thus creating a strong current that may contain chemical information about the female positioned at the first entrance (Atema, 1985, 1988). The pleopod fanning frequencies in males correlate with the frequencies of females checking the shelter. The existence of pheromones that control female choice and molting as well as male aggression was therefore assumed (Cowan and Atema, 1990; Atema, 1995; Bushman and Atema, 1997).

The possible exchange and use of different water currents during agonistic encounters has rarely been studied; but see Rohleder and Breithaupt (2000) for a preliminary study in the crayfish *Astacus leptodactylus*. To test the possibility that snapping shrimp use guided water currents as signals, we visualized and analyzed all water currents that the shrimp produced during their encounters with conspecifics of the same or different sex and in encounters with sympatrically living mud flat crabs (*Eurypanopeus depressus*).

Materials and Methods

We analyzed the behavior of 12 adult specimens of *Alpheus heterochaelis*, a species of snapping shrimp (6 males, 6 females; body size: 3.9 ± 0.4 cm, mean $\pm$ SD). Each animal was tested in an encounter with a conspecific of equal size of either the same or different sex, as well as in an encounter with a small crab (*Eurypanopeus depressus*; mean length and width of carapace: $1.6 \pm 0.2 \times 1.2 \pm 0.2$ cm, mean $\pm$ SD). All animals were caught in waters of the Gulf coast of Florida at the Florida State University Marine Laboratory near Panacea. Prior to the experiments the animals were labeled with small numbers designated for marking queen bees and were kept individually in perforated plastic containers ($11 \times 11 \times 15$ cm) containing gravel and oyster shells for shelter. The containers were placed within a large tank ($90 \times 195 \times 33$ cm) with 330 l of circulating filtered seawater (salinity: 23‰–28‰; temperature: 22°–23°C). Proteins were removed from the water, and pH, carbonate, oxygen, CO_2, and NO_3 were regularly controlled. The shrimp were exposed to an illumination cycle of 12 h light/12 h dark and fed frozen shrimp, fish, or mussels three times a week.

For visualization of the different water currents, we pre-

pared the aquarium water (temperature: 22°–24°C, water level: 5 cm) with small, floating plastic particles (ABS-particles, Bayer, Leverkusen, diameter: 500–710 μm; specific weight: 1.03 kg/l). The aquarium (30 × 24 × 24 cm; floor covered with black cloth to facilitate walking) was positioned on a platform isolated from vibrations (Breithaupt et al., 1995). At the level of the interacting animals, the seawater was illuminated from one side by a slide projector holding a slide with a thin horizontal slit. Before each experiment fresh seawater and particles were added, and two animals (two snapping shrimp or one snapping shrimp and a crab) were placed in the aquarium for 10 min for acclimatization; the animals were separated by an opaque divider to prevent visual, tactile, and directed-chemical contact. After the partition was removed, all interactions between the animals during the following 20 min were videotaped from above (camera: Panasonic AG 455; video recorder: Panasonic AG 7355; monitor: Sony Trinitron). The reflexive characteristics of the suspended particles then allowed a precise tracking using standard video-frame analysis.

Each experiment (interactions between two snapping shrimp of the same or different sex or between a snapping shrimp and a crab) was characterized by the number of physical contacts between the opponents, regardless of their duration and strength, as well as by the number of water jets. Three different water currents were characterized, including a lateral gill current, an anterior gill current, and a pleopod current (Fig. 1a). The pleopod current was measured only when the shrimp was not in locomotion, because this current is also likely to be used in supporting the animal's walking. Moreover, no current was included in our analysis unless the single-frame video analysis gave clear evidence that it had moved two or more plastic particles. The following parameters were evaluated for all visualized water currents: frequency, duration (time between onset of movement of the first floating particle and end of movement of the last particle), range (total distance covered by an identified particle due to a certain current; possibly underestimated when the current hit an opponent or an aquarium wall), velocity and target of the currents, their potential to transfer chemical information (i.e., entering the area of chemical perception at the receiver's side), the temporal correlation between currents and previous physical contacts, and the correlation between produced currents and water jets in winners and losers during intrasexual interactions. To determine a winner or loser, we counted the number of aggressive acts and the number of submissive acts after each physical contact between the conspecific opponents throughout the encounter. Aggressive acts include behaviors such as approach, aggressive stance, and grasping and opening of the claws. Submissive acts include moving backwards and turning and tail flipping away from the opponent. These definitions are largely adopted from Nolan and

Salmon (1970). In 11 out of 12 experiments, one animal produced more aggressive acts and fewer submissive ones than its opponent and was therefore determined to be the winner while the opponent was determined to be the loser.

Statgraphics Plus 6.0 (Manugistics Group, Inc.) and SPSS 6.0.1. (SPSS Science Software GmbH) were used for statistics. Mean and standard deviation were calculated for each variable of interest for each tested individual, and only one value per individual (grand mean) is included in each statistical test. The behavior of the respective opponents (male and female snapping shrimp, and crabs) was not analyzed and is not included in our results (exception: data presented in Fig. 7). If not otherwise stated, the Friedman rank test for repeated measurements (sample size >2) or the Wilcoxon rank test (sample size = 2) were used, and values with $P < 0.01$ and $P < 0.05$ are indicated in the text. We used nonparametric statistical tests because most of the data did not fulfill the requirements for the use of parametric tests i.e., normality or equal variance.

To gain more insight into the mechanism of gill current production and redirection, two snapping shrimp were tethered upside down in a small petri dish filled with seawater and floating plastic particles, and the activity of the different mouth parts, which produced or deflected the currents, was videotaped using a CCD camera (Sony XC-77CE) mounted on a binocular microscope with high magnification. In addition, small drops of black ink (Brilliant Black 4001, Pelikan) were placed between the third and fourth walking legs of these shrimp as well as of animals tethered dorsal side up to a vertical holder and standing on a platform so that the gill currents could be visualized. (Fig. 1b).

Results

Visualization of water currents in tethered shrimp

A unique feature of snapping shrimp is the production of an extremely rapid water jet by fast closure of a specialized snapper claw. Apart from this water jet, the snapping shrimp *Alpheus heterochaelis* is able to produce four kinds of water currents (Fig. 1), which can be subdivided into two main categories. Fanning of the pleopods causes a strong, posteriorly directed *pleopod current*, and a *gill current* is produced by rhythmically beating the scaphognathites as revealed by our visualization experiments in two tethered shrimp. Beating of the scaphognathites produces a depression in the gill chamber; water is therefore sucked into this chamber and subsequently released anteriorly through two small openings in the carapace. This "normal" gill current can be visualized with ink in tethered animals, but it is too slow and weak to move floating particles and was therefore not analyzed during encounters of snapping shrimp and their opponents. It can, however, be accelerated and deflected into a *lateral gill current* (see Fig. 1B) by the exopodites of the second and third maxillipeds. The expo-
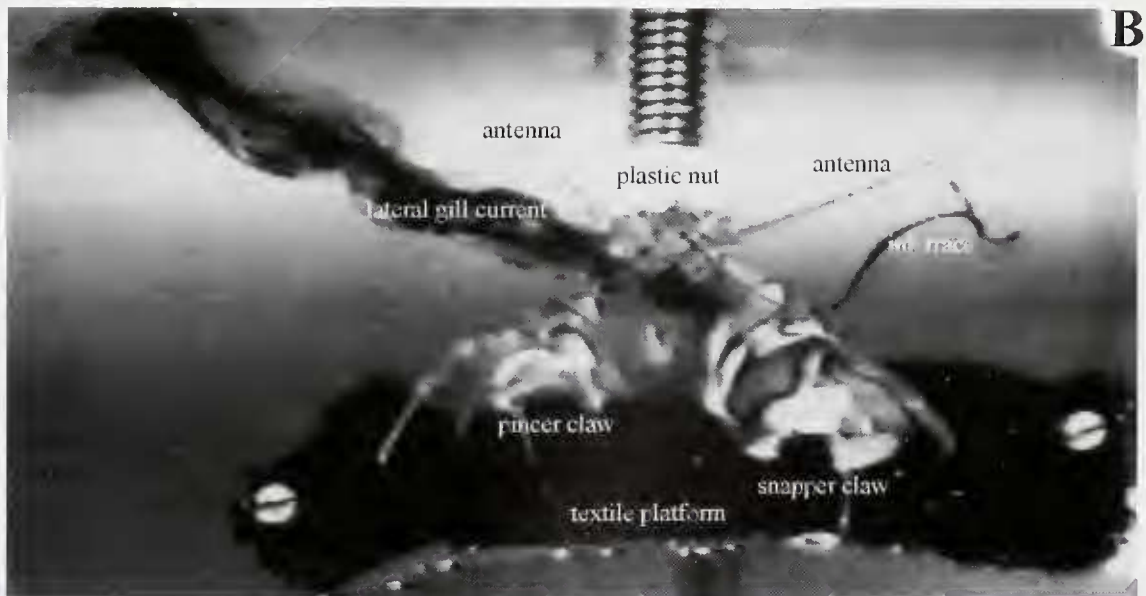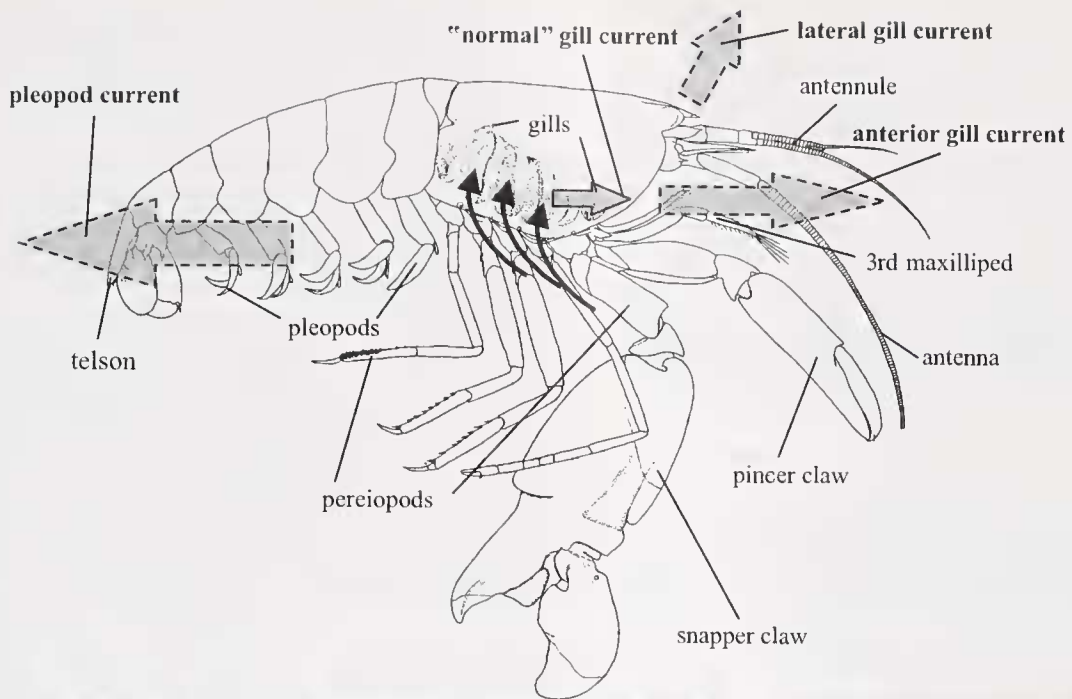
Figure 1. (A) Schematized drawing (lateral view) of a snapping shrimp modified after Kim and Abele (1988) showing four different water currents (gray arrows): the "normal" gill current, the lateral gill current, the anterior gill current, and the pleopod current. Black arrows show the direction of water entering the gill chamber. (B) Frontal view of an *Alpheus heterochaelis* snapping shrimp, tethered to a vertical holder by means of a plastic nut glued to the carapace and standing on a textile platform. Black ink was placed with a syringe between the third and fourth left pereiopods (see ink trace) to visualize the gill currents. The shrimp is fanning the exopodites of the right second and third maxillipeds, thus producing an ink-stained lateral gill current to the right.

dites of the first maxilliped do not participate in this process. Fanning of the left exopodites results in acceleration and deflection of the released gill current to the left side, and fanning of the right exopodites results in deflection to the right side. Tethered snapping shrimp never beat the exopodites of both sides simultaneously, and this was also never observed during interactions in which the illuminated particles were directed to only one side at a time. Interestingly,

Figure 2. Frequency of three different water currents (l-gc, lateral gill current, a-gc, anterior gill current, pc, pleopod current) produced by *Alpheus heterochaelis* snapping shrimp in interactions with another shrimp of the same sex (homo), of different sex (hetero), and with a *Eurypanopeus depressus* crab (inter). Grand means and standard deviations for 12 snapping shrimp each are shown. Significant differences within interaction types with $P < 0.01$ are indicated by two asterisks (**).

a *(fast) anterior gill current* was restricted to encounters of freely moving animals; it could not be elicited in tethered shrimp. Its production obviously requires physical, chemical, or visual contact between the animals. As a result, we were not able to analyze the producing mechanism; that is, we did not identify the involved mouth parts.

General characteristics of released water currents

Encounters between two snapping shrimp of different sex (hetero) are characterized by a significantly higher number of physical contacts (23.9 ± 8.3, $n = 287$; $P < 0.01$) than seen in encounters between two shrimp of the same sex (homo; 13.8 ± 6, $n = 165$), or between a snapping shrimp and a crab (*Eurypanopeus depressus*) (interspecific; 12.7 ± 5.3, $n = 157$). On the other hand, snapping (water jet production) of the tested shrimp is significantly increased after a contact with a crab ($38\% \pm 16\%$; $P < 0.01$) when compared to snapping after hetero and homo contacts ($5\% \pm 4\%$ and $11\% \pm 11\%$, respectively).

These differences in mind, we first evaluated the number of water currents (lateral gill currents, anterior gill currents, and pleopod currents) in each experiment. Figure 2 shows that there are no essential differences between interaction types (homo, hetero, or interspecific). Within each interaction type, however, the number of lateral gill currents significantly ($P < 0.01$) exceeds that of anterior gill currents as well as that of pleopod currents. In addition, in interspecific encounters with a crab, the frequency of anterior gill currents is significantly lower than the frequency of pleopod currents ($P < 0.01$).

The duration of the different water currents (Fig. 3A) tends to be longest for lateral gill currents, with no significant differences regarding the type of the opponent. The duration of anterior gill currents is generally shorter, with similar values in intraspecific interactions, yet almost twice as long as in interactions with a small crab. Anterior gill currents in interspecific encounters are significantly shorter in duration than lateral gill currents ($P < 0.05$). Pleopod currents, in contrast, reveal very consistent values for all types of interactions.

Figure 3B shows the range of the different currents in all interaction types. Regardless of the opponent, the snapping shrimp tend to produce lateral gill currents with small ranges. Anterior gill currents generally cover larger distances in intraspecific interactions, whereas the mean value is reduced in interactions with a crab. The most powerful current is the pleopod current, which covers long distances in all interaction types. Range differences within interaction types are significant at $P < 0.05$ and $P < 0.01$, respectively.

The velocity of the water currents during the first 120 ms (6 video frames) was evaluated for 10 examples for each current and interaction type (Fig. 3C). There are no significant differences in the velocities within and between different types of interactions. The lateral gill current shows the slowest velocities in all encounters. The anterior gill current and the pleopod current show similar values and are both more powerful than the lateral gill current. Initial velocities are higher, but their analysis has not proved satisfactory because of the standard video time resolution of 20 ms (50 frame/s).

Temporal relation of water currents to physical contact

Figure 4 compares the frequency of water currents that were elicited within 10 s after a physical contact between the opponents with those that were "spontaneously" produced—that is, emitted more than 10 s after a preceding contact. As shown in Figure 4A, in all interaction types the lateral gill current is significantly more often produced spontaneously than following a physical contact ($P < 0.01$). In homo interactions it occurs in only 6.2% of all cases ($n = 10$ of 162) shortly after a contact. During hetero interactions this current is elicited by a contact in 11.5% of all cases ($n = 21$ of 183); in interactions with a crab, the lateral gill currents occur within 10 s after a contact in only 8.5% of all cases ($n = 13$ of 153).

The analysis of the anterior gill current reveals a completely different frequency pattern, with more elicited currents than spontaneous ones (Fig. 4B). In homo interactions the anterior gill current is produced in 65.5% of all cases ($n = 19$ of 29) within 10 s after a preceding contact. Similarly, in hetero interactions this gill current is elicited by a contact in 62.5% of all cases ($n = 15$ of 24). Finally, during interactions with a crab, anterior gill currents are

A

B

C
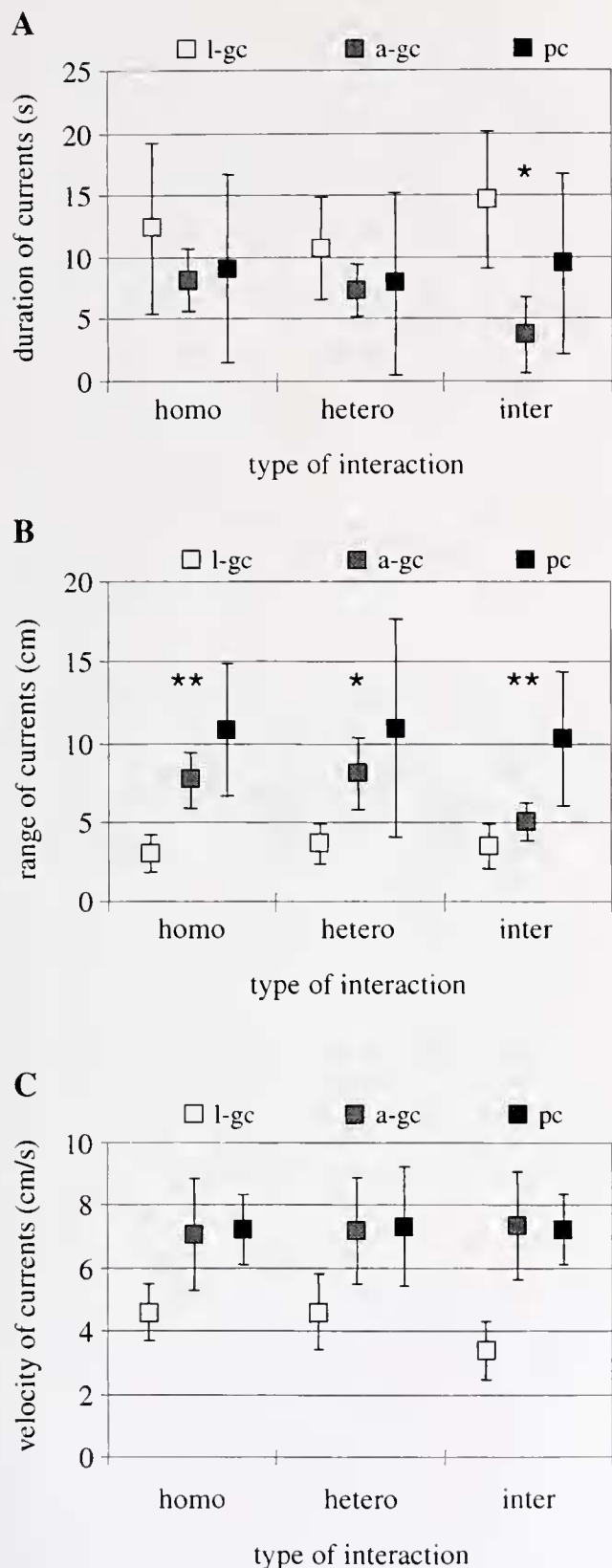
Figure 3. Duration (A), range (B), and velocity (C) of the lateral gill current (l-gc), the anterior gill current (a-gc), and the pleopod current (pc) in interactions of two snapping shrimp of the same sex (homo), of different

released within 10 s after a contact in 78.6% of all cases ($n = 11$ of 14).

In contrast, the pleopod current, like the lateral gill current, is significantly more often ($P < 0.01$) produced without an immediately preceding contact in all types of interactions (Fig. 4C). During homo interactions we observed only 7.7% of pleopod currents within 10 s after the last contact ($n = 4$ of 52). In hetero interactions this current is elicited in 16.7% of all cases ($n = 8$ of 48) by a preceding contact, and in interspecific interactions there are 13.0% of pleopod currents shortly after a previous contact ($n = 7$ of 54).

### Possible chemosensory information transfer by water currents

If any of the water currents were used to transfer chemical information, one would expect them to be directed toward the chemoreceptive antennules of the opponent. We therefore evaluated the number of currents that reached the area between the opponents' claws—that is, an area mostly covered by the flicking antennules. This was possible by analyzing the video sequences and identifying the area of particle dispersion with respect to the animals' position. In fact, only the anterior gill current seems qualified to fulfill the function of possible information transfer (Fig. 5).

In all types of interactions, the mean number of lateral gill currents that miss the antennules is significantly higher ($P < 0.01$) than the mean number of those hitting the target (Fig. 5A). In homo interactions the lateral gill current reaches the antennule area in only 0.6% of the cases ($n = 1$ of 162). During hetero interactions lateral gill currents are never directed toward the opponent's antennules, but hit other targets ($n = 183$). In interactions with a crab, the snapping shrimp produce 0.7% ($n = 1$ of 153) of lateral gill currents, which could possibly transfer chemical information.

In comparison, a higher percentage of anterior gill currents reaches the antennule area in all interaction types (Fig. 5B). During homo interactions the anteriorly projected gill current reaches the antennules of the opponent in 35.7% of all cases ($n = 10$ of 28). In hetero interactions the percentage (66.7%, $n = 16$ of 24) of anterior gill currents directed toward the antennules is even higher than that of undirected anterior gill currents. During interspecific interactions the snapping shrimp projects 35.7% anterior gill currents toward the antennules of the crab ($n = 5$ of 14).

The frequency pattern for pleopod currents is similar to

sex (hetero), and of a snapping shrimp and a crab (inter). Grand means and standard deviations for 12 shrimp are shown in A and B; means and standard deviations of the velocity during the first 120 ms of 10 currents each are shown in C. A significant difference within an interaction type with $P < 0.05$ is indicated by one asterisk (*) and with $P < 0.01$ by two asterisks (**).

A

B

C

A

B

C
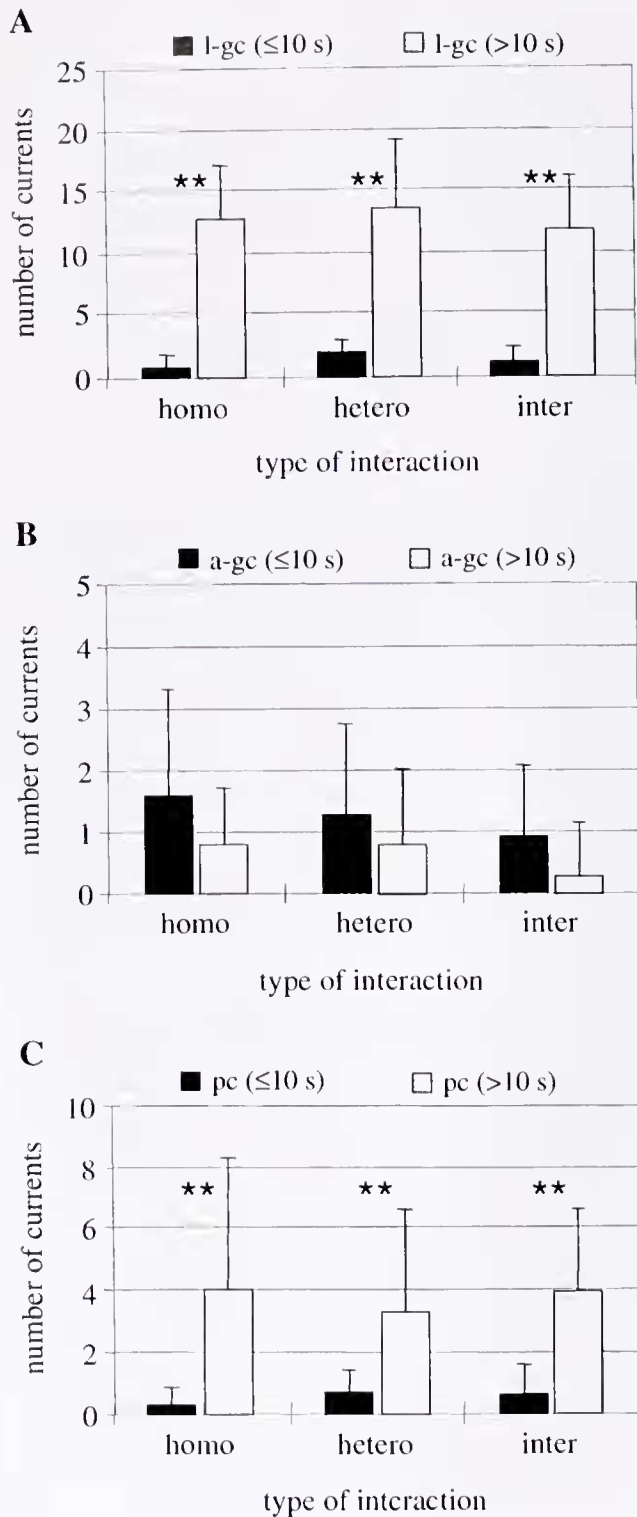
Figure 4. Mean number of lateral gill currents (A), anterior gill currents (B), and pleopod currents (C) within 10 s (black columns) or more than 10 s (white columns) after a physical contact between the opponents in interactions of two snapping shrimp of the same sex (homo), of different sex (hetero), and of a snapping shrimp and a crab (inter). Grand means and standard deviations for 12 shrimp are shown. Significant differences with $P < 0.01$ are indicated by two asterisks (**).
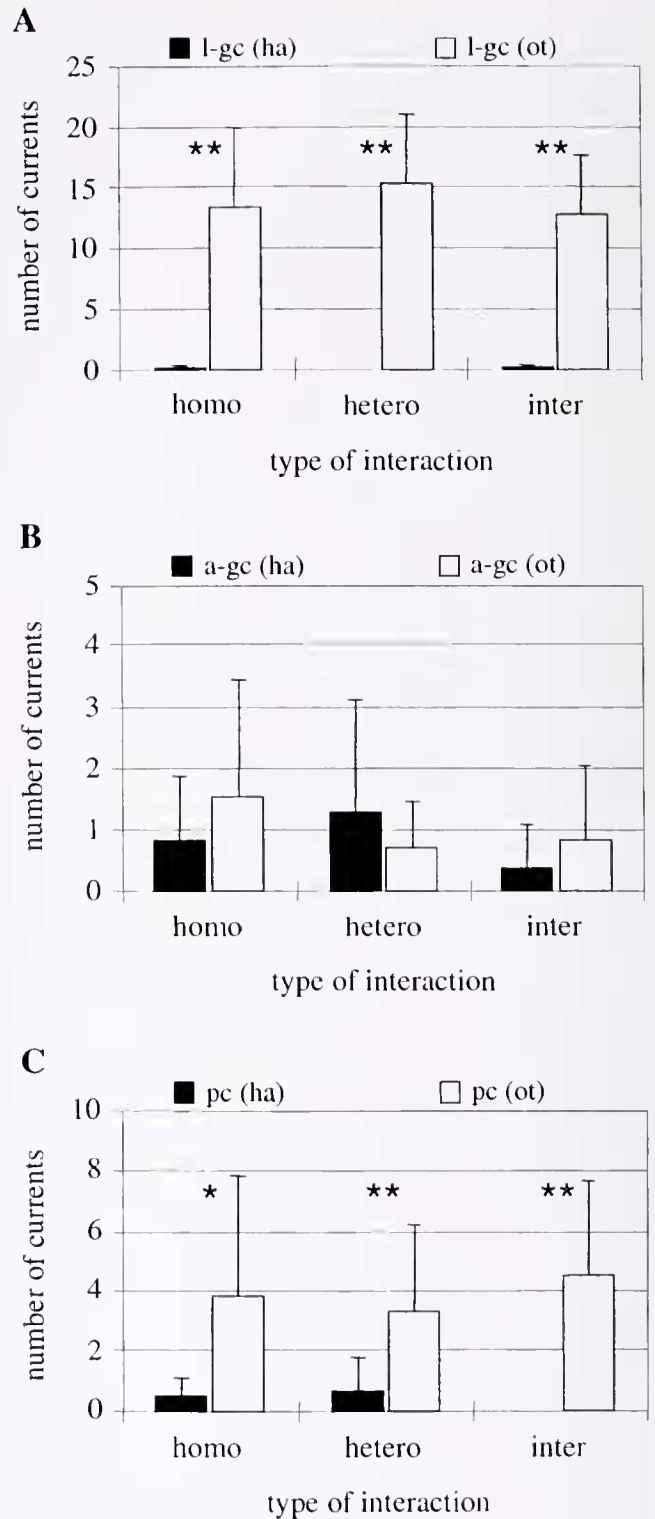
Figure 5. Mean number of lateral gill currents (A), anterior gill currents (B), and pleopod currents (C) hitting the antennules of the opponent (black columns, ha) or reaching other targets (white columns, ot) in interactions of two snapping shrimp of the same sex (homo), of different sex (hetero), and of a snapping shrimp and a crab (inter). Grand means and standard deviations for 12 shrimp are shown. A significant difference with $P < 0.05$ is indicated by one asterisk (*) and with $P < 0.01$ by two asterisks (**).
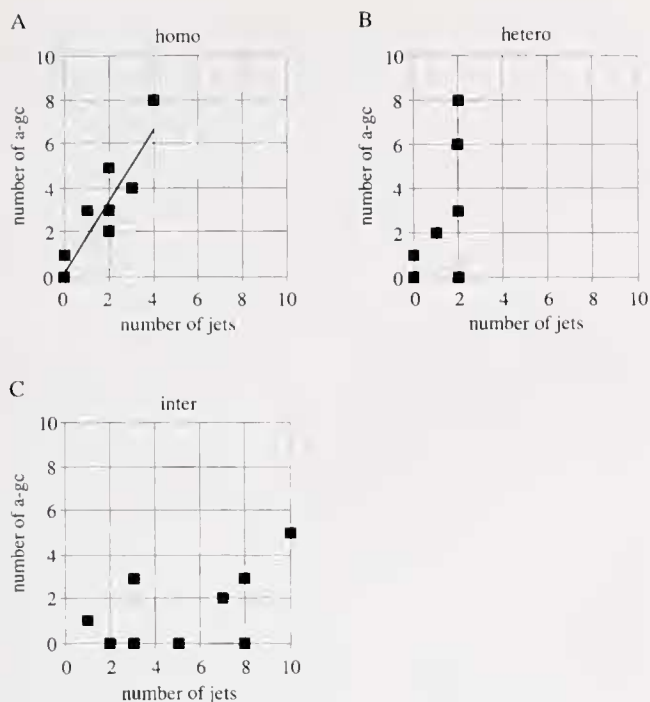
Figure 6. Correlation between the number of water jets and the number of anterior gill currents produced in interactions of two snapping shrimp (A) of the same sex (homo; Spearman's coefficient of rank correlation $r_s = 0.9$, $P < 0.01$), (B) of different sex (hetero), and (C) of a snapping shrimp and a crab (inter). Data of 12 shrimp each—some data points overlap.

that of lateral gill currents; the undirected currents significantly exceed the antennule-directed ones in each interaction type ($P < 0.05$ or 0.01, respectively; Fig. 5C). In homo interactions an average of only 11.5% ($n = 6$ of 52) of all pleopod currents are projected towards the chemoreceptive antennules, and during hetero interactions 16.7% ($n = 8$ of 48) of all pleopod currents reach the antennule area. Finally, in interspecific interactions no pleopod current is aimed towards the antennules of the crab, but all ($n = 54$) are directed elsewhere.

Anterior gill currents and water jets

In view of the prominent role of the anterior gill current with respect to its timing after a physical contact and the increased possibility of chemosensory information transfer, we tested the correlation between these gill currents and emitted water jets (Fig. 6). As mentioned before, in comparison to intraspecific interactions, encounters with crabs are characterized by an increased number of water jets and a reduced number of anterior gill currents (Fig. 6C). In addition, more water jets are emitted in homo interactions between snapping shrimp (Fig. 6A) than in hetero encounters (Fig. 6B). Thus, the number of anterior gill currents significantly increases with an increasing number of water

jets only in interactions between two snapping shrimp of the same sex (Spearman rank correlation coefficient: $r_s = 0.9$, $P < 0.01$; Fig. 6A). This is not the case in interactions between two shrimp of different sex ($r_s = 0.5$, $P > 0.05$), though a noticeable trend is shown and the overall low number of water jets may have prevented a significant result. An even lower degree of correlation is seen in interactions with a crab ($r_s = 0.4$, $P > 0.1$).

As shown in Figure 7, winners of homo interactions (as defined by aggressive and submissive acts—see Materials and Methods) not only produce a significantly higher mean number of water jets ($N = 11$, $P < 0.01$) but also a significantly higher mean number of anterior gill currents than losers produce ($N = 11$; $P < 0.01$).

Discussion

Snapping shrimp (*Alpheus heterochaelis*) produce two main water currents, a strong posteriorly directed pleopod current and an anteriorly directed gill current. We show that the "normal" anteriorly directed gill current can be modified and redirected into a lateral and a fast anterior gill current. The production of the latter is restricted to social interactions, in which it represents a powerful tool for chemical signaling. Moreover, the use of the fast anterior gill currents varies for the winners and losers of individual encounters.

Mechanisms of gill current production

Our experiments in tethered snapping shrimp show that water is sucked into the gill chamber due to a depression elicited by the beating scaphognathites (Fig. 1A). A "normal" gill current is then released anteriorly with low velocity through two small openings of the carapace. Once the left or right expodites of the second and third maxillipeds start fanning, the current is accelerated and deflected laterally to that side (Fig. 1B). As previously described in
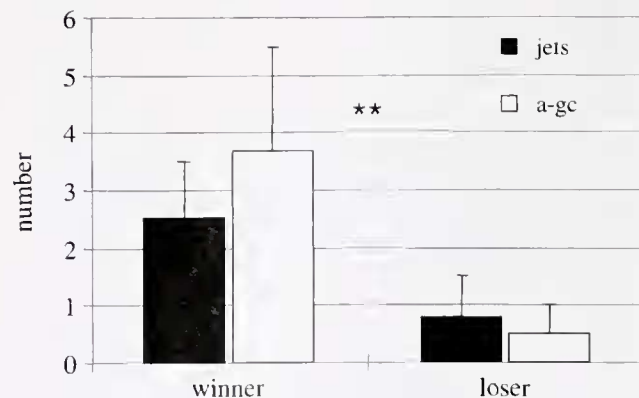
Figure 7. Frequency of water jets (jets, black columns) and anterior gill currents (a-gc, white columns) for winners and losers in interactions of two snapping shrimp of the same sex. The significant differences between winners and losers with $P \leq 0.01$ are indicated by two asterisks (**).

lobsters (*Homarus americanus*), the exopodites of the first maxillipeds do not contribute to these lateral gill currents in snapping shrimp, whereas in crayfish (*Procambarus clarkii*) these appendages are also involved (Breithaupt, 1998).

The production mechanism of the fast anterior gill current remains unclear, since this behavior obviously requires physical, chemical, or visual contact during intra- or interspecific encounters of snapping shrimp, and thus was never seen in tethered animals. From our knowledge about the lateral gill current, we assume that the fast anterior gill current is created by high-frequency beating of the scaphognathites without contribution of the exopodites of the second and third maxillipeds. Since it is difficult to video-record the mouth parts with high magnification during social interactions, we are currently testing other methods of monitoring scaphognathite beating frequencies during encounters to verify this hypothesis.

Role of the fast anterior gill current during social interactions

The analysis of the fast anterior gill current revealed the most surprising and interesting results. Although anterior gill currents were observed and well described in lobsters (Atema, 1985, 1995) and crayfish (Breithaupt, 1998), we found decisive differences in snapping shrimp. First of all, *Alpheus heterochaelis* produces different types of anterior gill currents. The "normal" anterior current is a slow, weak release of water, which was sucked through the gill chamber, as opposed to the fast, strong, anteriorly directed gill current, which occurs during social interactions. The production of the fast anterior gill current is rare (Fig. 2) but strongly linked to previous contacts with a conspecific or a crab (Fig. 4B). Among the observed currents, only the fast anterior current is created shortly *after* a preceding contact, regardless of the type of opponent. In fact, this current never occurred *before* the first contact. Moreover, we show that only this current is suited to transfer chemical information towards the other animal (Fig. 5B): it reaches the antennules of the opponent in nearly 50% of all cases.

Of all analyzed currents, only the fast anterior gill current shows some peculiarities with respect to the shrimps' opponent. The number, duration, and range is smaller in encounters with a crab than in interactions with conspecifics (Figs. 2, 3). We assume that the shrimp collect information about the genus of their opponent and reduce the effort to communicate accordingly, if it is a crab.

Role of lateral gill currents during social interactions

During social interactions between snapping shrimp and conspecifics of the same or different sex as well as during interactions with small crabs, the lateral gill currents are most prominent and significantly outnumber all other observed currents (*i.e.,* pleopod currents and fast anterior gill currents; Fig. 2). Moreover, they are produced for long intervals but have a short range and a low velocity (Fig. 3). They are barely elicited by physical contact (Fig. 4A) and hardly ever reach the antennules of their opponents (Fig. 5A). These properties of the lateral gill currents do not change with different opponents but appear to result from a stereotyped form of production. Thus, obviously lateral gill currents are not predestined to play a prominent role in active (chemical) signaling between the animals.

Still, their function needs explanation. From our observations we conclude that the lateral gill current is used to improve the shrimps' ability to sense possible odor signals that occur at close distance. By redirecting the "normal" gill current, the shrimp refreshes the area around its chemical receptors from its own smell (released by the slow and permanent gill current) and thereby improves the detection of the chemical surrounding. This idea is supported by our knowledge that *Alpheus heterochaelis* naturally inhabits small, oyster-shell-covered areas with little water flow and that individuals of the species appear to be rather stationary within that area (Herberholz and Schmitz, pers. obs.). The lateral gill current produced by snapping shrimp seems to be used to remove water from the area around the antennules and to a much lesser extent to draw water toward that region as proposed for the posteriorly or laterally redirected gill currents of lobsters and crayfish (Atema, 1995; Breithaupt, 1998). In contrast to lobsters and crayfish, snapping shrimp were never observed to fan simultaneously with appendages on both sides. Instead, they beat the exopodites of *one* side at a time, and there are no obvious movements of particles from the opposite side toward the animal's anterior region.

Role of pleopod currents during social interactions

In lobsters (*Homarus americanus*), pleopod currents are used for chemical (possibly pheromonal) communication during courtship at a shelter (Atema, 1985, 1988, 1995; Cowan and Atema, 1990; Bushman and Atema, 1997). The snapping shrimp *Alpheus heterochaelis,* in addition to using its pleopods for locomotion and to provide an oxygen supply for attached eggs, uses them for shelter digging, fanning the substrate (sand or muddy-sand) backward behind it (Nolan and Salmon, 1970). These authors also mention (pleopod) fanning as an aggressive act, with a shrimp vigorously beating its pleopods and directing a water current posteriorly quite close to another shrimp. The frequency of pleopod fanning is not noted by Nolan and Salmon (1970), but the behavior was described to occur between two females at the entrance of a shelter. In our experiments, we did not provide a shelter, and all shrimp were in the middle of their molt cycle. In view of the finding that the actual impact of pleopod currents in lobsters depends to a high degree on the molt state of the animals as well as on their readiness to mate (Cowan and Atema, 1990), these condi-

tions may have affected our results. Though pleopod currents were rather often produced (Fig. 2) and (in comparison to gill currents) show an average duration, a large range, and high velocity (Fig. 3), there is a lack of correlation with previous contacts (Fig. 4C) and a low precision in hitting the antennules of the opponent (Fig. 5C). There are hardly any differences in the characteristics of these currents towards different opponents. All this indicates that pleopod currents are of little relevance for (chemical) signaling or communication among snapping shrimp and between shrimp and sympatric crabs under our conditions.

A specialized gill current for chemical signaling and communication?

The transfer of chemical signals between interacting lobsters (see *e.g.*, Atema, 1995; Bushmann and Atema, 1997) and crayfish (Breithaupt *et al.*, 1999) has been described in detail. In lobsters these signals can evoke long-term individual recognition (Karavanich and Atema, 1998a, b), and in crayfish they communicate dominance status or stress condition (Zulandt Schneider *et al.*, 1999; Zulandt Schneider and Moore, 2000). In all cases, urine-borne signals were assumed to be the source of chemical signaling (Breithaupt *et al.*, 1999; Breithaupt, pers. comm.). Since the urine is released through a paired set of nephropores on the ventral sides of the basal segments of the second antennae (Parry, 1960), it can be carried toward an opponent by the anterior gill current. Moreover, agonistic behavior in catheterized lobsters increases the probability and volume of urine release (Breithaupt *et al.*, 1999).

In the present study we show for the first time that the pattern of water current production actually changes with respect to the social situation of an aquatic animal. Although snapping shrimp have the ability to produce "normal" anterior gill currents, they create different, more powerful, anteriorly directed gill currents shortly after contacting their interaction partner. These elicited currents are then more likely to reach the opponents' area of chemical perception. The same may hold true for lobsters and crayfish, but their currents have not yet been quantified during social interactions. On the other hand, we still have to prove that the fast anterior gill current in snapping shrimp actually carries chemical signals toward the opponent. Although the data presented favor this assumption, we cannot exclude the possibility that hydrodynamic signals transferred by the gill currents participate in the communication between the animals. Judging by their sensory equipment, snapping shrimp—like crayfish (Mellon, 1996) and lobsters (Guenther and Atema, 1998; Weaver and Atema, 1998)—are most likely to perceive hydrodynamic stimuli as well as chemical stimuli with their antennules (Schmitz, unpubl.). We plan to test this possibility by deactivating the chemical receptors only.

In any case, the production of the fast anterior gill current may play a critical role during hierarchy formation in snapping shrimp. We show that in intrasexual encounters the numbers of water jets and anterior gill currents are positively correlated (Fig. 6) and that both are significantly higher in the winner than in the loser (Fig. 7). In the present study, winner and loser met in only a single 20-min experiment. Preliminary experiments show that repetitive pairing of winners and losers reduces the number of water jets and anterior gill currents (Obermeier and Schmitz, unpubl.). This supports the finding that these behaviors are most probably correlated with dominance and social status in snapping shrimp. Although the strength of the water jet represents the strength of the animal (see Herberholz and Schmitz, 1999), the signal transferred by the gill current may then allow recognition of the sender. This, in turn, can prevent two *Alpheus heterochaelis* shrimp of the same sex from engaging in more severe fighting during subsequent encounters, thus reducing the number of the "costly" water jets.

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